

# Genetic association of lint yield with its components in cotton chromosome substitution lines

Jixiang Wu · Johnie N. Jenkins · Jack C. McCarty ·  
Sukumar Saha · Richard Percy

Received: 31 January 2008 / Accepted: 30 April 2008 / Published online: 16 May 2008  
© Springer Science+Business Media B.V. 2008

**Abstract** Dissection of the genetic relationship between lint yield and its yield components at the chromosome level may provide an additional avenue for yield enhancement in cotton (*Gossypium hirsutum* L.). Based on the conditional additive-dominance (AD) genetic model, we investigated the genetic structures of lint yield with its three component traits, lint percentage, boll weight, and boll number, using a two-location data set containing cotton chromosome substitution lines (chromosome or chromosome arm substituted from *G.*

*barbadense* L. into *G. hirsutum* L., TM-1) which are defined as CS-B lines and their F<sub>2</sub> hybrids with CS-B recurrent parent TM-1. We calculated the conditional variance components, contribution ratios, and contribution effects subject to the additive and dominant components. Our results showed that boll number or boll number with boll weight greatly reduced the conditional variance components and phenotypic variance for lint yield and thus indicated that boll number plays a more important role in lint yield than the other two component traits. We demonstrated that the *G. barbadense* chromosomes in CS-B16, CS-B18, and CS-B4sh were directly associated with reduced lint yield. Substituted chromosome arms 14sh, 22sh, and 22Lo were associated with reduced additive effects for lint yield through the component of boll weight, thus suggesting that some substituted chromosomes or chromosome arms may be indirectly associated with lint yield through yield component traits. This study provides a better understanding of cotton yield and its component traits at the chromosome level and this information should be useful in cotton breeding.

---

Mention of trade names or commercial products in this manuscript does not imply recommendations or endorsement by the U.S. Department of Agriculture.  
Joint contribution of USDA, ARS and Mississippi State University. Journal paper No. J11277 of Mississippi Agricultural and Forestry Experiment Station.

---

J. Wu (✉)  
Department of Plant and Soil Sciences, Mississippi State University, P.O. Box 9555, Mississippi State, MS 39762, USA  
e-mail: jixiang.wu@ars.usda.gov

J. N. Jenkins · J. C. McCarty · S. Saha  
Crop Science Research Laboratory, United States Department of Agriculture, Agricultural Research Service (USDA-ARS), P.O. Box 5367, Mississippi State, MS 39762, USA  
e-mail: johnie.jenkins@ars.usda.gov

R. Percy  
United States Department of Agriculture, Agricultural Research Service, 2881 F&B Rd., College Station, TX 77845, USA

**Keywords** Yield components · Conditional model · Chromosome substitution lines · Cotton

## Introduction

Cotton (*Gossypium* spp. L.) lint yield is made up of component traits of boll number, lint percentage, and

boll weight. A better understanding of the genetic relationship between yield and its components should be useful in cotton breeding.

Correlation analysis can be used to detect the phenotypic relationship between yield and its component traits. Multiple linear regression analysis can reveal single or joint contribution from component traits to a complex trait (Myers 1990). Path analysis can partition the simple correlation coefficients into direct and indirect effect on the target trait (Wright 1920) and this method was applied in rice (Samonte et al. 1998) and bean (Bora et al. 1998; Ball et al. 2001). Worley et al. (1974, 1976) reported that boll number per unit land area was the largest contributor to lint yield. Maintaining a high lint percentage was also important to ensure high lint yield (Culp and Harrell 1975). Several approaches have been proposed for analyzing the relationships between a complex trait and its multiplicative component traits (Sparnaaij and Bos 1993; Melchinger et al. 1994; Piepho 1995). Covariance component analyses have shown that cotton lint yield is dependent on the three yield components; however, the additive or dominance genetic effects vary among traits (Wu et al. 1995; Tang et al. 1996; McCarty et al. 1998).

The classic multiple linear regression model assumes that the independent variables are fixed. However, the yield components are usually measured with random errors thus they cannot satisfy the assumption required by the linear regression model. The conditional multiple linear regression model proposed by Jobson (1991) can be used for this type of analysis. Under many circumstances, both yield and its component traits are affected by genotypic effects, environmental effects, and genotype  $\times$  environment interaction effects as well (Wu et al. 1995; Tang et al. 1996; McCarty et al. 1998, 2004). When a complex genetic model is involved, the correlation method, path analysis, or conditional linear regression methods mentioned above can not be used for the proper analysis of genetic effects.

The variation due to one or more component traits can be mathematically removed, and the remaining variation (conditional variance) can be calculated accordingly (Graybill 1976; Krzanowski 1988; Jobson 1991; Zhu 1995; Wu et al. 2004, 2006; Wen and Zhu 2005). Thus, the amount of variation due to individual or combinations of several component traits can be calculated (Zhu 1995; Wu et al. 2004, 2006). Using the

model developed by Zhu (1995), the conditional variance components and conditional effects can be calculated for both developmental traits like rate of flowering and complex traits like lint yield. Bolls per plant accounted for about 45% of the variation in lint yield with additive and additive by environment interaction effects, while 2% of the variation was due to dominance and dominance by environment interaction effects (Zhu 1995). However, Zhu's conditional model can only analyze individual component traits. If yield component traits are independent, then Zhu's conditional model can be repeatedly used for these independent component traits. However, several reports showed that yield components have significant genetic correlations (Wu et al. 1995; Tang et al. 1996; McCarty et al. 1998), thus greatly complicating a multivariable conditional analysis. Wen and Zhu (2005) extended Zhu's model to bivariate conditional analysis. Wu et al. (2004, 2006) further extended Zhu's conditional model from a single component trait to include multiple component traits with a genotype and genotype  $\times$  environment (GE) model. Based on the results from a recombinant inbred (RI) population containing 188 lines, they found that boll number and lint percentage, or boll number and boll weight combinations accounted for more than 80% of the contributions to both genotypic and GE variations in lint yield. Ninety-nine percent of the genetic and phenotypic variations in lint yield could be accounted for by these three component traits (Wu et al. 2004). Wu et al. (2006) also provided a recursive approach for analyzing multivariate conditional variances and conditional effects under a general linear model. With this model, the contribution effects of component trait(s) to a complex trait can also be calculated. Thus, the conditional approach provides a way to dissect complex genetic relationships between a complex trait and its component traits for different genetic models. The applications of this approach to the additive and dominance (AD) genetic model have not been reported.

In this study, 14 chromosome substitution lines were crossed with their recurrent parent TM-1 and 14  $F_2$  hybrids and their parents were planted at two locations in 2002. The two-location data set consisting of lint yield and three yield components were analyzed by the generalized conditional model proposed by Wu et al. (2006) subject to the AD genetic model (Cockerham 1980; Zhu 1994). Conditional

variance components for lint yield on yield component trait(s) and their contribution ratios to lint yield from yield component(s) were calculated. The contribution effects through yield component traits were also determined. Thus, this study provides a better understanding of the genetic relationships between yield and yield components that should provide valuable genetic information for yield improvement in future breeding programs. In a prior study (Saha et al. 2006) specific chromosome effects on yield were analyzed using the AD model; however, in the present study we focus on the dissection of complex genetic relationships between lint yield and its three component traits using the conditional AD model. We only use two environments where  $F_2$  hybrids and parents were included in the current study.

## Materials and methods

### Experimental materials

Fourteen near-isogenic euploid ( $2n = 52$ )  $BC_5S_1$  chromosome substitution (CS-B) lines containing different pairs of *G. barbadense* chromosomes or segments were used as male parents and crossed to the recurrent parent, TM-1 and  $F_2$  hybrids were developed. In each CS-B line, a single chromosome pair of TM-1 has been replaced by the corresponding part of the 3-79 (*G. barbadense*) genome. These CS-B lines are designated by the chromosome number specific to the introgressed chromosome or chromosome arm of the alien species as follows, CS-B02, CS-B04, CS-B06, CS-B07, CS-B16, CS-B17, CS-B18, CSB-25, CS-B5sh (sh = short arm), CS-B14sh, CS-B15sh, CS-B22sh, CS-B22Lo (Lo = long arm), and CS-B26Lo.

The development of these CS-B lines was described in previous studies (Saha et al. 2004; Stelly et al. 2005). TM-1 is an inbred line derived from the commercial variety Deltapine 14 and maintained over 40 generations by selfing (Kohel et al. 1970). Crosses were made at Mississippi State in the summer of 2000.  $F_1$  plants were grown at a winter nursery in Tecoman, Mexico to produce  $F_2$  hybrid seeds.

The same 14  $F_2$  hybrids, TM-1, 3-79, and all parental CS-B lines (except CS-B26Lo due to seed shortage), were grown in MS (location 1) and AZ (location 2) in field plots using a randomized complete block design with four replicates in 2002

(Saha et al. 2006). Standard production practices were followed in the growing season for the two locations. A 25-boll hand-harvested sample was collected from each plot prior to machine picking. These samples were weighed to determine boll weight and ginned on a laboratory 10-saw gin to determine lint percentage. The plots were machine harvested, and seed cotton was weighed. Boll number per hectare was calculated by dividing seed cotton yield by boll weight (Tang et al. 1996). Lint yield per hectare was determined by multiplying seed cotton yield by lint percentage.

Since 3-79 is not an adapted cultivar in Mississippi and flowers late and is abnormally low in yield, the data set we used for conditional and other analysis excluded 3-79 and its  $F_2$  hybrid with TM-1.

### Genetic models and statistical methods

An additive-dominance (AD) with GE interaction genetic model was used for our data analysis (Zhu 1994; Wu et al. 1995; Tang et al. 1996; Saha et al. 2006). The genetic model for parent  $i$  at environment  $h$  is expressed as follows,

$$y_{hiik(P)} = \mu + E_h + 2A_i + D_{ii} + 2AE_{hi} + DE_{hii} + B_{k(h)} + e_{hiik} \quad (1)$$

The genetic model for the  $F_2$  hybrid between parents  $i$  and  $j$  at environment  $h$  is expressed as follows,

$$y_{hijk(F_2)} = \mu + E_h + (A_i + A_j) + (0.25D_{ii} + 0.25D_{jj} + 0.5D_{ij}) + (AE_{hi} + AE_{hj}) + (0.25DE_{hii} + 0.25DE_{hjj} + 0.5DE_{hij}) + B_{k(h)} + e_{hijk}$$

where,  $\mu$  = population mean,  $E_h$  = environmental effect,  $A_i$  or  $A_j$  are the additive effects,  $D_{ii}$ ,  $D_{jj}$ , or  $D_{ij}$  are the dominance effects,  $AE_{hi}$  or  $AE_{hj}$  are the additive-by-environment interaction effects,  $D_{hii}$ ,  $D_{hjj}$ , or  $D_{hij}$  are the dominance-by-environment interaction effects,  $B_{k(h)}$  is the block effect, and  $e_{hijk}$  is random error.

With this AD model and the recursive approach proposed by Wu et al. (2006) conditional and unconditional variance components were estimated by MINQUE (1), in which all prior values were set as 1.0 (Zhu 1989). Conditional and unconditional effects were predicted by an adjusted unbiased prediction (AUP)

approach (Zhu 1993). The unconditional and conditional phenotypic variance ( $V_P$ ) was defined as follows,  $V_P = V_A + V_D + V_{AE} + V_{DE} + V_e$  where,  $V_A = 2\sigma_A^2$  for additive effects,  $V_D = \sigma_D^2$  for dominance effects,  $V_{AE} = 2\sigma_{AE}^2$  for additive by environment interaction effects,  $V_{DE} = \sigma_{DE}^2$  for dominance by environment effects, and  $V_e = \sigma_e^2$  for random errors. The quantity  $1.0 - V_{P(LY|component(s))}/V_{P(LY)}$  is defined as the phenotypic contribution ratio  $CR_{P(component(s) \rightarrow LY)}$  from single or multiple component traits. The quantity  $1.0 - \sigma_{u(LY|component(s))}^2/\sigma_{u(LY)}^2$  is defined as the contribution ratio  $CR_{u(component(s) \rightarrow LY)}$  from single or multiple component traits for the  $u$ th random effect (Zhu 1995; Wu et al. 2004, 2006). The ratio  $(\sigma_{u(LY)}^2 - \sigma_{u(LY|component(s))}^2)/V_{P(LY)}$  is defined as the proportional contribution ratio  $PCR_{u(component(s) \rightarrow LY)}$  to the phenotypic variance in lint yield from single or more component traits for the  $u$ th random effect (Wu et al. 2004, 2006). The vector  $\mathbf{e}_{u(LY)} - \mathbf{e}_{u(LY|component(s))}$  is defined as the  $u$ th contribution effect vector,  $\mathbf{e}_{u(component(s) \rightarrow LY)}$ , from single or joint yield components to lint yield. Resampling (the jackknifing) method was applied to calculate the standard error (SE) for each parameter by removal of each block within environment (Miller 1974). An approximate  $t$ -test (degrees of freedom = 7) was used to detect the significance of each parameter and 95% confidence intervals were used to test the difference among parameters. All data analyses were conducted using a self-written program in C++ (Wu et al. 2004, 2006).

## Results

Phenotypic correlations among lint yield and its components

Lint percentage was significantly correlated with boll weight and boll number in each location (Table 1). Boll weight and boll number were significantly correlated with lint yield for both locations.

Estimated variance components for yield and yield component traits

Additive and dominance effects and their GE interaction effects were significant for lint percentage (Table 2). Dominance effects were predominant among all genetic effects. Both AD effects influenced

**Table 1** Phenotypic correlation coefficients among yield and yield components

	BW	BN	LY
Loc = 1			
LP	−0.26**	−0.28**	−0.09
BW		−0.12	0.27**
BN			0.87**
Loc = 2			
LP	−0.29**	−0.20*	−0.06
BW		0.08	0.38**
BN			0.92**

LP = lint percentage, BW = boll weight, BN = boll number, and LY = lint yield

\* and \*\* significant at 0.05 and 0.01, respectively

boll weight and their GE interaction effects were also significant for this trait. Additive effects and dominance  $\times$  environment interaction effects were significant for boll number per hectare. Additive effects, dominance effects, and dominance  $\times$  environment interaction effects were significant for lint yield. On average, the genotypic variance components were more important than GE variance components for lint percentage and boll weight. However, it is not surprising that the  $G \times E$  interaction effects played a more important role than genotypic effects for boll number and lint yield (Table 2) because the environmental conditions in these two locations are very different. The results indicated that the genetic performances for boll number and lint yield were more dependent on specific environmental conditions. The residual effects accounted for 5.7%, 24%, 24.6%, and 21.1% of the phenotypic variances for lint percentage, boll weight, boll number, and lint yield, respectively.

Conditional variance components and contribution ratios to lint yield

The  $u$ th conditional variance for lint yield for a given component trait(s) measures the amount of the  $u$ th variance in lint yield not accounted for by the component trait(s) (Wu et al. 2004). For example, the conditional additive variance component for lint yield given lint percentage measures the additive variance in lint yield without influence of lint percentage. Compared with the unconditional

**Table 2** Estimated variance components for lint yield and yield components

	LP	BW	BN	LY
$V_A$	$0.97 \pm 0.17^{**}$	$0.056 \pm 0.014^{**}$	$2921 \pm 1279$	$8564 \pm 2902^*$
$V_D$	$2.98 \pm 0.38^{**}$	$0.086 \pm 0.032^*$	$0 \pm 0$	$8020 \pm 3858$
$V_{AE}$	$0.27 \pm 0.06^{**}$	$0.005 \pm 0.003$	$0 \pm 0$	$0 \pm 0$
$V_{DE}$	$0.40 \pm 0.15^*$	$0.054 \pm 0.016^*$	$12533 \pm 2601^{**}$	$30592 \pm 8824^*$
$V_e$	$0.28 \pm 0.03^{**}$	$0.064 \pm 0.016^{**}$	$5036 \pm 793^{**}$	$12623 \pm 3441^{**}$
$V_P$	$4.90 \pm 0.28^{**}$	$0.265 \pm 0.016^{**}$	$20489 \pm 2635^{**}$	$59799 \pm 6240^{**}$

LP = lint percentage,  
BW = boll weight,  
BN = boll number, and  
LY = lint yield

\* and \*\* significant at 0.05  
and 0.01, respectively

**Table 3** Contribution ratios of yield component traits to lint yield

	LP	BW	BN	LP&BW	LP&BN	BW&BN	LP&BW&BN
$V_A$	$0.63 \pm 0.08$	$0.14 \pm 0.15$	$0.93 \pm 0.16$	$0.82 \pm 0.04$	$0.93 \pm 0.16$	$0.96 \pm 0.16$	$1.00 \pm 0.00$
$V_D$	$0.00 \pm 0.16$	$0.32 \pm 0.16$	$0.57 \pm 0.16$	$0.00 \pm 0.18$	$0.63 \pm 0.17$	$0.92 \pm 0.18$	$1.00 \pm 0.00$
$V_{AE}$	$0.00 \pm 0.18$	$0.00 \pm 0.00$	$0.00 \pm 0.18$	$0.00 \pm 0.18$	$0.00 \pm 0.18$	$0.00 \pm 0.18$	$0.00 \pm 0.18$
$V_{DE}$	$0.36 \pm 0.15$	$0.00 \pm 0.16$	$0.91 \pm 0.12$	$0.35 \pm 0.15$	$0.94 \pm 0.12$	$0.96 \pm 0.16$	$0.97 \pm 0.12$
$V_e$	$0.00 \pm 0.00$	$0.00 \pm 0.03$	$0.82 \pm 0.12$	$0.00 \pm 0.02$	$0.84 \pm 0.12$	$0.95 \pm 0.04$	$0.97 \pm 0.04$
$V_P$	$0.19 \pm 0.06$	$0.05 \pm 0.05$	$0.85 \pm 0.02$	$0.25 \pm 0.05$	$0.87 \pm 0.02$	$0.95 \pm 0.01$	$0.97 \pm 0.00$

LP = lint percentage, BW = boll weight, BN = boll number, and LY = lint yield

variances for lint yield, the conditional variances (both variance components and phenotypic variance) for lint yield given boll number were much smaller than those given lint percentage or boll weight (data not shown). For example, 7% (594/8564) of additive variance in lint yield was not explained by boll number. Thirty seven percent (3130/8564) and 86% (7391/8564) of additive variance in lint yield was not accounted for by lint percentage and boll weight, respectively, indicating that 93%, 63%, and 14% of additive variance for lint yield was accounted for by boll number, lint percentage, and boll weight, respectively. Conditional additive variance for lint yield given lint percentage by boll weight, lint percentage by boll number, or boll number with boll weight was greatly reduced from the unconditional additive variance for lint yield, suggesting that lint percentage with boll weight, lint percentage with boll number, and boll number with boll weight were responsible for the majority of the additive variance in lint yield (Tables 2 and 3). The conditional dominance variance for lint yield given lint percentage, or lint percentage with boll weight was slightly but not significantly greater than the unconditional dominance variance for lint yield. The conditional dominance variance for lint yield given boll weight was not significant lower than the unconditional dominance variance for lint yield.

The results implied that lint percentage, boll weight or lint percentage with boll weight had no significant contribution to the dominance variance for lint yield. The conditional dominance variances for lint yield given boll number, lint percentage by boll number, and boll weight with boll number were significant, indicating that boll number, or boll number with other component traits made major and significant contribution to the dominance variance for lint yield, especially for boll number with boll weight or boll number with boll weight and lint percentage. No single component traits or combinations of traits made significant contributions to additive by environment interaction variance for lint yield. The conditional variance of dominance by environment interaction for yield given boll number or boll number with other component traits was significantly reduced, suggesting that boll number or boll number with other one or two yield components made the major contribution to the variance of dominance by environment interaction for yield.

In summary, boll number or boll number with other yield components greatly reduced the conditional variance components and phenotypic variance for lint yield. Thus, the data suggested that boll number plays a more important role in lint yield than the other two component traits.

### Contribution genetic effects of yield component traits to lint yield

Additive and dominant contribution effects to lint yield were predicted. Since additive effects are equivalent to general combining ability and can be used for line selection, we only listed the unconditional additive effects and additive contribution effects to lint yield through yield component traits (Table 4). Squared correlation coefficients between unconditional additive effects for lint yield and additive contribution effects to lint yield were close

to the additive contribution ratios listed in Table 4, indicating that the additive contribution effect prediction agreed with the contribution ratio estimation.

The results showed that the CS-B lines differed in term of the unconditional additive effects for lint yield (Table 4). Based on the 95% confidence interval test, CS-B02, CS-B04, CS-B15sh were higher than CS-B16, CS-B18, and CS-B14sh with respect to additive effects for lint yield. The significant difference in additive effects between any two CS-B lines is due to the additive effects on two chromosomes. The significant difference in additive

**Table 4** Unconditional additive effects (kg/ha) for lint yield and additive contribution effects (kg/ha) of component traits to lint yield

	LY <sup>a</sup>	LP → LY	BW → LY	BN → LY
CS-B02	29.14 ± 13.86*	4.90 ± 21.34	14.04 ± 3.33**	11.32 ± 19.95
CS-B04	53.57 ± 26.77	25.92 ± 22.30	20.85 ± 5.86**	41.32 ± 29.17
CS-B06	30.62 ± 23.95	17.78 ± 11.35	39.68 ± 9.35**	9.35 ± 27.80
CS-B07	15.08 ± 17.13	8.08 ± 10.13	21.85 ± 4.49**	-1.61 ± 21.36
CS-B16	-92.59 ± 29.62*	-34.60 ± 44.45	10.24 ± 15.99	-97.83 ± 28.97*
CS-B17	20.09 ± 17.66	12.87 ± 10.50	-0.38 ± 3.35	42.21 ± 21.25
CS-B18	-141.95 ± 39.11**	-54.20 ± 62.44	-21.19 ± 17.63	-129.72 ± 40.18*
CS-B25	25.64 ± 16.17	11.84 ± 10.71	-12.97 ± 7.75	49.78 ± 17.47*
CS-B05sh	15.60 ± 12.61	4.81 ± 10.42	-10.80 ± 5.80	17.32 ± 15.06
CS-B14sh	-70.86 ± 28.75*	-20.86 ± 40.42	-53.07 ± 12.09*	-27.02 ± 40.02
CS-B15sh	46.41 ± 17.22*	19.25 ± 21.05	35.95 ± 7.45**	25.92 ± 22.31
CS-B22sh	-18.31 ± 21.83	-27.40 ± 14.40	-14.04 ± 2.97**	-33.10 ± 19.43
CS-B22Lo	48.93 ± 31.89	5.64 ± 38.69	-53.03 ± 21.80**	52.02 ± 29.53
CS-B26Lo	-26.00 ± 42.82	-12.18 ± 21.48	-4.20 ± 2.60	-13.99 ± 42.04
TM-1	64.80 ± 21.95*	38.26 ± 18.19	27.11 ± 6.72**	54.14 ± 23.18
	LP&BW → LY	LP&BN → LY	BW&BN → LY	LP,BW&BN → LY
CS-B02	30.01 ± 7.40**	14.74 ± 17.16	17.96 ± 13.55	29.14 ± 13.86
CS-B04	58.08 ± 11.16**	41.52 ± 28.34	53.21 ± 25.39	53.57 ± 26.77
CS-B06	41.25 ± 16.55*	10.90 ± 24.55	30.07 ± 22.54	30.62 ± 23.95
CS-B07	22.09 ± 11.58	0.39 ± 19.89	11.62 ± 17.12	15.08 ± 17.13
CS-B16	-81.39 ± 48.79*	-96.53 ± 28.51*	-92.13 ± 27.51*	-92.59 ± 29.62*
CS-B17	7.90 ± 17.28	32.00 ± 18.60	41.23 ± 17.33*	20.09 ± 17.66
CS-B18	-130.13 ± 46.55*	-131.53 ± 40.16*	-143.01 ± 38.39**	-141.95 ± 39.11**
CS-B25	15.78 ± 23.88	43.25 ± 14.02*	41.50 ± 18.16	25.64 ± 16.17
CS-B05sh	10.90 ± 16.61	18.50 ± 14.04	14.48 ± 14.06	15.60 ± 12.61
CS-B14sh	-67.97 ± 20.28*	-30.60 ± 33.32	-55.08 ± 30.31	-70.86 ± 28.75*
CS-B15sh	48.92 ± 6.53**	26.59 ± 19.65	46.66 ± 16.82*	46.41 ± 17.22*
CS-B22sh	-26.76 ± 9.72*	-26.58 ± 19.36	-37.74 ± 19.31	-18.31 ± 21.83
CS-B22Lo	45.95 ± 47.71	59.64 ± 27.88	25.27 ± 30.35	48.93 ± 31.89
CS-B26Lo	-32.68 ± 22.33	-17.40 ± 38.82	-19.86 ± 43.64	-26.00 ± 42.82
TM-1	58.16 ± 14.85**	55.21 ± 22.97*	65.90 ± 22.03*	64.80 ± 21.95*

<sup>a</sup> Unconditional additive effects for lint yield predicted by the AD model, the remaining columns are contribution effects predicted by the AD model  
\* and \*\* significant from zero at 0.05 and 0.01, respectively



effects between a CS-B line and TM-1 is due to the substituted chromosome additive effect. In this study, we observed that three CS-B lines, CS-B16, CS-B18, and CS-B14sh, were less than TM-1 subject to additive effects for lint yield, indicating that three substituted chromosomes or arm 16, 18, and 14sh of 3-79 were associated with reduced lint yield. This agrees with Saha et al. (2006) data from the analysis of the AD model using five-environment data.

In the same way, a significant difference in additive contribution effects between a CS-B line and TM-1 suggested that the substituted chromosome is responsible for the difference due to one or more component traits associated with that substituted chromosome. For example, boll weight in CS-B14sh, CS-B22sh, and CS-B22Lo made lower contribution effects to lint yield compared to TM-1, indicating these three substituted chromosome arms were associated with reduced additive effects for lint yield due to boll number. CS-B16 and CS-B18 had lower additive contribution effects to yield due to boll number, or boll number with lint percentage or with boll weight than TM-1, indicating that boll number, or boll number with lint percentage or boll weight associated with genes on these two substituted chromosomes for reducing lint yield. Boll number related to substituted chromosome arm 14sh did not make significant additive effect contribution to lint yield. Additive contribution effects to lint yield due to lint percentage with boll weight for CS-B16, CS-B18, and CS-B14sh were less than those for TM-1, suggesting that these three chromosomes or chromosome arm made reduced additive contribution to lint yield due to lint percentage with boll weight compared to TM-1. Additive contribution effects were the same as the additive effects for lint yield and thus it suggests that these three component traits made full contribution to lint yield in terms of additive effects. Thus, the contribution effects help explain how the components of lint yield affect lint yield. The analysis used by Saha et al. (2006) detected effects of specific chromosomes on yield, but could not explain how yield components were associated with lint yield.

## Discussion

It is possible to use CS-B lines to identify genetic factors associated with specific chromosomes or chromosome arms for a quantitative trait because

each CS-B line is isogenic to its recurrent parent except it has one chromosome or chromosome arm different (Saha et al. 2004). With the AD genetic model (Zhu 1994) each quantitative trait can be determined to associate with specific chromosomes or chromosome arms in terms of additive and/or dominance effects including GE interaction effects (Saha et al. 2006; Jenkins et al. 2006, 2007; McCarty et al. 2006). In this study, we focused on the dissection of complex genetic relationships between lint yield and its three component traits using the AD model (Cockerham 1980; Zhu 1994; Wu et al. 1995; Tang et al. 1996) and with the conditional approach (Wu et al. 2004, 2006).

The conditional AD genetic model in this study was an extension of the genotype model (Wu et al. 2004, 2006). With the chromosome substitution lines we were able to detect conditional variance components, contribution ratios, and contribution effects subject to the additive and dominant components at the chromosome level. Our results revealed that boll number or boll number with the other yield components greatly reduced the conditional variance components and phenotypic variance for lint yield and thus indicated that boll number plays a more important role in lint yield than the other two component traits. Results showed that chromosome substituted chromosomes 16 and 18 and short arm 14sh were associated with reduced additive effects for lint yield compared to TM-1 (Table 4 this study). The results agreed with our previous reports (Saha et al. 2004, 2006; Jenkins et al. 2006). The substituted chromosome arms 14sh, 22sh, and 22Lo were associated with reduced additive effects for lint yield compared to TM-1 due to boll weight. The substituted chromosome arm 22Lo did not have direct association with additive effect for reduced yield due to boll number or boll number with lint percentage or with boll weight. The results above indicate that some substituted chromosomes or chromosome arms are not directly associated with lint yield yet they may be indirectly associated with lint yield due to one or more yield component traits. On the other hand, substituted chromosomes 16 and 18 contributed low additive effects for lint yield due to boll number and substituted chromosome arm 14sh contributed negative additive effect due to boll weight or boll weight with lint percentage. Thus, the results suggest that the chromosomes associated with lint yield may affect

yield by a single component trait or several component traits.

With the chromosome substitution based RI populations and more DNA markers developed, the QTLs controlling yield and yield component traits may be identified. With the conditional model approach, we can more precisely identify the conditional QTLs for lint yield given one or more yield component traits. Such studies will provide a more detailed genetic structure between yield and its component traits. Further investigation remains in this area.

## References

- Ball RA, McNew RW, Vories ED, Keisling TC, Purcel LC (2001) Path analyses of population density effects on short-season soybean yield. *Agron J* 93:187–195
- Bora GC, Gupta SN, Tomer YS, Singh S (1998) Genetic variability, correlation and path analysis in faba bean (*Vicia faba*). *Indian J Agric Sci* 68:212–214
- Cockerham CC (1980) Random and fixed effects in plant genetics. *Theor Appl Genet* 56:119–131
- Culp TW, Harrell DC (1975) Influence of lint percentage, boll size, and seed size on lint yield of upland cotton with high fiber strength. *Crop Sci* 15:741–746
- Graybill FA (1976) Theory and application of linear model. Duxbury, Boston
- Jenkins JN, Wu J, McCarty JC, Saha S, Gutierrez OA, Hayes R, Stelly DM (2006) Genetic effects of thirteen *Gossypium barbadense* L. chromosome substitution lines in topcrosses with upland cultivars: yield and yield components. *Crop Sci* 46:1169–1178
- Jenkins JN, McCarty JC, Wu J, Saha S, Gutierrez OA, Hayes R, Stelly DM (2007) Genetic effects of Genetic effects of thirteen *Gossypium barbadense* L. chromosome substitution lines in topcrosses with upland cultivars: fiber quality traits. *Crop Sci* 47:561–572
- Jobson JD (1991) Applied multivariate data analysis volume II: categorical and multivariate methods. Springer-Verlag, New York
- Kohel RJ, Richmond TR, Lewis CF (1970) Texas marker-1. Description of a genetic standard for *Gossypium hirsutum* L. *Crop Sci* 10:670–671
- Krzanowski WJ (1988) Principles of multivariate analysis. Oxford Science Publications, New York
- Melchinger AE, Singh M, Link W, Utz HF, von Kitzlitz E (1994) Heterosis and gene effects of multiplicative characters: Theoretical relationships and experimental results from *Vicia faba* L. *Theor Appl Genet* 88:343–348
- McCarty JC, Jenkins JN, Zhu J (1998) Introgression of day-neutral genes in primitive cotton accessions: I. Genetic variances and correlations. *Crop Sci* 38:1425–1428
- McCarty JC, Jenkins JN, Wu J (2004) Primitive accession germplasm by cultivar crosses as sources for cotton improvement I: phenotypic values and variance components. *Crop Sci* 44:1226–1230
- McCarty JC, Wu J, Saha S, Jenkins JN, Hayes R (2006) Effects of chromosome 5sh from *Gossypium barbadense* L. on flower production in *G. hirsutum* L. *Euphytica* 152:99–107
- Miller RG (1974) The jackknife: a review. *Biometrika* 61:1–15
- Myers RH (1990) Classical and modern regression with applications. PWS-KENT Publishing Company, Boston
- Piepho HP (1995) A simple procedure for yield component analysis. *Euphytica* 84:43–48
- Saha S, Wu J, Jenkins JN Jr, McCarty JC, Gutiérrez OA, Percy RG, Raska DA, Stelly DM (2004) Association of agronomic and fiber traits with specific Pima 3-79 chromosomes in a TM-1 Background. *J Cotton Sci* 8:162–169
- Saha S, Jenkins JN, Wu J, McCarty JC, Percy RG, Cantrell RG, Stelly DM (2006) Effect of chromosome specific introgression in Upland cotton on fiber and agronomic traits. *Genetics* 172:1927–1938
- Samonte SOP, Wilson LT, McClung AM (1998) Path analyses of yield and yield-related traits of fifteen diverse rice genotypes. *Crop Sci* 38:1130–1136
- Sparnaajj LD, Bos I (1993) Components analysis of complex characters in plant breeding I. Proposed method for qualifying the relative contribution of individual components to variation of the complex characters. *Euphytica* 70:225–235
- Stelly DM, Saha S, Raska DA, Jenkins JN, McCarty JC, Gutierrez OA (2005) Registration of 17 germplasm lines of upland cotton (*Gossypium hirsutum*), each with a different pair of *G. barbadense* chromosome or chromosome arms substituted for the respective *G. hirsutum* chromosome or chromosome arms. *Crop Sci* 45:2663–2665
- Tang B, Jenkins JN, Watson CE, McCarty JC, Creech RG (1996) Evaluation of Genetic variances, heritabilities, and correlations for yield and fiber traits among cotton F<sub>2</sub> hybrid populations. *Euphytica* 91:315–322
- Wen Y, Zhu J (2005) Multivariable conditional analysis for complex trait and its components. *Acta Genet Sin* 32(3):289–296
- Worley S, Culp TW, Harrell DC (1974) The relative contributions of yield components to lint yield of upland cotton, *Gossypium hirsutum* L. *Euphytica* 23:399–403
- Worley S, Ramey HH, Harrell DC, Culp TW (1976) Ontogenetic model of cotton yield. *Crop Sci* 16:30–34
- Wright S (1920) The relative importance of heredity and environment in determining the piebald pattern of guinea-pigs. *Proc Natl Acad Sci USA* 6:320–332
- Wu J, Zhu J, Xu F, Ji D (1995) Analysis of genetic effect by environment interactions for yield traits in upland cotton (Chinese). *Heredita* 17(5):1–4
- Wu J, Jenkins JN, McCarty JC, Zhu J (2004) Genetic associations of yield with its component traits in a recombinant inbred line population of cotton. *Euphytica* 140:171–179
- Wu J, Wu D, Jenkins JN, McCarty JC (2006) A recursive approach to detect multivariable conditional variance components and conditional random effects. *Comput Stat Data Anal* 50:285–300
- Zhu J (1989) Estimation of genetic variance components in the general mixed model. PhD Dissertation, North Carolina State University, Raleigh, USA (Diss abstract. DA 8924291)



- Zhu J (1993) Methods of predicting genotype value and heterosis for offspring of hybrids. *J Biomath (Chinese)* 8(1):32–44
- Zhu J (1994) General genetic models and new analysis methods for quantitative traits (Chinese). *J Zhejiang Agric Univ* 20:551–559
- Zhu J (1995) Analysis of conditional effects and variance components in developmental genetics. *Genetics* 141:1633–1699